

HABITAT CHARACTERIZATION OF SECONDARY CAVITY-NESTING BIRDS IN OKLAHOMA

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ABSTRACT.—We analyzed vegetation structure at potential and actual nest sites of secondary cavity-nesting birds in south-central Oklahoma. Habitats consisted of old fields with remnants of tallgrass prairie and patches of post oak-blackjack oak (*Quercus stellata*, *Q. marilandica*) woodland. During the 1989 and 1990 breeding seasons, 194 sites with nest boxes were analyzed, including those occupied by Bewick's Wrens (*Thryomanes bewickii*), Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P. bicolor*), Eastern Bluebirds (*Sialia sialis*), House Sparrows (*Passer domesticus*), and some not used by birds. Principal-components analysis was employed to describe general vegetational gradients and stepwise discriminant analysis to delineate differences in nest-site habitats among species. Through use of appropriate indices and Monte Carlo simulations, niche breadth and overlap were assessed relative to a habitat gradient (principal component I) extending from open areas to woodlands. Chance expectations were established assuming that the nest boxes represented a limited resource, albeit one that was not fully utilized during the course of the study. Eastern Bluebirds and House Sparrows chose nest boxes in open areas with few trees, Bewick's Wrens selected boxes in wooded areas with junipers and few deciduous trees other than oaks, Carolina Chickadees most often were found in areas with junipers and oaks, and nest boxes used by Tufted Titmice were broadly distributed, not showing association with any particular habitat type. Niche overlap for Eastern Bluebirds and House Sparrows was more pronounced than expected by chance. These two species showed less overlap with Bewick's Wrens, Carolina Chickadees, and Tufted Titmice than expected given simulation results. For the House Sparrow and Eastern Bluebird, which were restricted to open habitats, niche breadth was significantly less than expected by chance. Likewise, niche breadth for the Bewick's Wren, with the majority of its nests being in semiopen areas, was less than predicted. For Carolina Chickadees and Tufted Titmice, nest-box use relative to the habitat gradient represented by principal component I was not different from random expectations. Our findings indicate that the introduced House Sparrow potentially can negatively influence nesting success of Eastern Bluebirds given that preferences for nest sites of the two species correspond so closely. Direct observations of House Sparrow and Eastern Bluebird interactions indicate that in some cases bluebirds are detrimentally affected. Received 11 Feb. 1993, accepted 15 Oct. 1993.

Habitat can be defined in a narrow sense as a spatially contiguous vegetation type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types (Hutto 1985). Avian habitats include foraging, singing and nesting sites that can be defined by their associated structural and floristic properties. James (1971) assessed habitats of breeding birds on the basis of several structural attributes of the vegetation, which taken together describe the "niche-gestalt" for a species. A number of studies have shown strong associations between

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bird-species occurrence and structural aspects of the vegetation (e.g., MacArthur and MacArthur 1961, James 1971, Rotenberry 1981, James and Wamer 1982). Habitat selection in birds has been thought to be a result of a species' response to the configuration of the vegetational components of the environment (e.g., Hilden 1965, Ficken and Ficken 1966, Klopfer 1969, Wiens 1969, Cody 1985).

Early quantitative studies of avian habitats described vegetation characteristics of plots centered on perches of singing territorial males (e.g., James 1971, Whitmore 1975, Smith 1977). In addition, some investigators have evaluated foraging and nesting sites within the breeding territory (e.g., Morrison and Meslow 1983, Willner et al. 1983, Holway 1991, Sakai and Noon 1991). Although the breeding habitats characterized by data from song-perch sites may provide a useful perspective, habitat evaluation of other bird activity sites is of interest to compare and contrast aspects of habitat use. Collins (1981) found that areas at song-perch sites and those at nest sites differed significantly for several warbler species. His and subsequent studies have shown that characteristics of nesting sites of avian species, in addition to those for other activity sites, can provide a more complete picture of avian breeding habitats.

Cavity-nesting birds provide an ideal group for evaluating nesting habitats. For example, Conner and Adkisson (1976, 1977) quantitatively assessed habitat use by woodpecker species, delineating important macrohabitat properties and those of microhabitats in the vicinity of nest cavities. Many secondary cavity-nesting birds (i.e., those that do not excavate their own cavities) readily use nest boxes. One can appraise nesting-habitat preferences of these species by describing immediate nest-box surroundings. Here we evaluate the habitat use of five secondary cavity-nesting bird species in south-central Oklahoma: Bewick's Wren (*Thryomanes bewickii*); Carolina Chickadee (*Parus carolinensis*); Tufted Titmouse (*P. bicolor*); Eastern Bluebird (*Sialia sialis*); and House Sparrow (*Passer domesticus*). Our purpose is to use interspecific comparisons to provide a more complete understanding of the important factors influencing habitat use by cavity-nesting species. The study design also allows us to assess indirectly possible influences of an introduced species, the House Sparrow, on nesting of native birds.

METHODS

Study sites.—Five sites (254 ha total) in two areas were studied during the 1989 and 1990 breeding seasons. One area, containing a single study site (64 ha), was on the grounds of the University of Oklahoma Biological Station (UOBS) in Marshall County. The second area included four study sites (190 ha total) and was located 11.3 km northeast of Ada, Pontotoc County, Oklahoma, approximately 118 km north of the first area. The four sites near Ada varied in size from 16 to 120 ha. All sites were characterized as old fields con-

taining remnants of tallgrass prairie, woody plants (including eastern red cedars, *Juniperus virginianus*, and winged elms, *Ulmus alata*), and patches of post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) woodland. Based on a preliminary quantitative assessment of vegetation data, as well as our familiarity with the two study areas, it was clear that they were very similar in vegetation characteristics; thus, data were combined for analyses. These sites were selected because they were representative of typical habitats of the region.

Nest boxes were classified as having been used by a bird species if nest building was completed and egg laying begun. The remaining boxes were categorized as unoccupied. For the UOBS site, which was evaluated only in 1989, 12 nest boxes were used: Bewick's Wren, 2 boxes; Carolina Chickadee, 1; Tufted Titmouse, 2; Eastern Bluebird, 5; and House Sparrow, 2. For the Ada sites, 182 potential nest sites were evaluated for habitat characteristics (see below) in the 1989 and 1990 breeding seasons, including nest boxes used by Bewick's Wrens (16), Carolina Chickadees (14), Tufted Titmice (17), Eastern Bluebirds (45), and House Sparrows (7), as well as 83 unoccupied boxes in 1990. Thirty-two nest boxes were used by more than one species during the breeding season and, thus, were entered into the analysis twice. Given that we have been conservative in our interpretation of statistical tests, this procedure is not likely to have significantly altered our conclusions.

Sampling techniques.—Nesting habitats were assessed by evaluating vegetation characteristics of 0.04-ha (0.1-acre) circular plots centered on 162 nest boxes placed in predetermined locations along the forest edge in south-central Oklahoma. The nest boxes (Oklahoma Dept. of Wildlife Conservation Nongame Program, 1986 pamphlet) had internal dimensions of 10.2 × 10.2 × 25.4 cm, with an entrance hole 3.8 cm in diameter. Nest boxes were placed on metal T-posts 1.2 to 1.5 m above the ground with the entrance hole oriented in a random direction. The circular-plot method developed by James and Shugart (1970) was used to quantify vegetation structure of the area surrounding the nest boxes. Each 0.04-ha circular plot was centered on a nest box. We also monitored the boxes weekly and recorded the number of eggs laid and hatched, as well as the number of young fledged.

Within each plot, we recorded (1) number of trees with diameters at breast height (dbh) greater than or equal to 7.6 cm; (2) number of shrub stems (<7.6 cm dbh) intercepted by a 1.52-m rod passed horizontally through vegetation at a height of 1 m along two orthogonal transects; and (3) ground-cover types at 20 points spaced 2 m apart along two orthogonal axes. The orientation of orthogonal axes for each plot was chosen randomly (using a random-number table). We calculated relative densities, basal areas and relative dominances (see Table 1) for several categories of trees including oaks, other deciduous tree species, and junipers. We also calculated shrub stem counts per unit area and percent ground cover.

To obtain vertical profiles of the vegetation, we passed a 7.5-m telescoping pole vertically through the vegetation at 20 points spaced 2 m apart along two orthogonal axes. We recorded the number of decimeter intervals with tree hits for 11 height-class intervals. At each of the 20 points, we also recorded the maximum height of the canopy. The vegetational inventories were completed at nest boxes during a six-week period from 21 May to 7 July in 1989 and 1990. The 40 vegetation variables evaluated and their abbreviations are listed in Table 1.

Principal-components analysis.—We employed principal-components analysis to characterize general trends along orthogonal vegetational gradients. Calculations were carried out using the computer package NT-SYS (Rohlf et al. 1982). From a matrix of correlations among 40 vegetation variables, major trends were represented on composite principal-component axes (Sneath and Sokal 1973). The first three components are orthogonal composite axes that explain progressively the maximum possible portion of the remaining character variance. None of the remaining principal components had eigenvalues greater than 3.00. Correlations (i.e., loadings) of original variables with principal components were generated, and component scores of each sample plot were projected onto the components. Before

TABLE 1

VEGETATION VARIABLES COMPUTED FOR NESTING-HABITAT PLOTS. VARIABLE NUMBER, CODE, DESCRIPTION, AND UNITS OF MEASURE GIVEN^a

No.	Code	Vegetation variable
1-3	OAKA-OAKC	Number of oaks with dbh >7.5-22.5 cm, >22.5-52.5 cm, and >52.5 cm, respectively (/ha)
4-6	NONA-NONC	Number of nonoaks with dbh >7.5-22.5 cm, >22.5-52.5 cm, and >52.5 cm, respectively (/ha)
7	JUNA	Number of junipers with dbh >7.5 cm (/ha)
8-10	DENSO, DENSN, DENSJ	Relative density of oaks, nonoaks, and junipers (percent = 100[no. oaks/total no. trees])
11-13	BAOAK, BANON, BAJUN	Basal area of oaks, nonoaks, junipers (cm ² /ha)
14-16	RDOAK, RDNON, RDJUN	Relative dominance of oaks, nonoaks, junipers (percent = 100[basal area oaks/total basal area])
17	VARQUAD	Variation (SD) in trees per quadrant (cm ² /ha)
18-22	STEMO, STEMN, STEMJ, STEMV	Number of oak, nonoak, juniper and vine stems at 1.5-m height (/ha)
22-27	WOODYCOV, FORBCOV, GRASSCOV, LEAFCOV, ROCKCOV, BARECOV	Ground cover of woody plants, forbs, grasses, leaf litter, rocks, or bare (percent)
28-38	HITSA-HITSK	Number of decimeters with tree hits, respectively, in the following height interval: 0.0-0.5 m; >0.5-1.0 m; >1.0-1.5 m; >1.5-2.0 m; >2.0-2.5 m; >2.5-3.0 m; >3.0-3.5 m; >3.5-4.5 m; >4.5-5.5 m; >5.5-6.5 m; >6.5-7.5 m (circle)
39	CANHT	Mean maximum height of canopy (m)
40	VARCAN	Variation (SD) of maximum height of canopy (cm ² /ha)

^a Arcsine transformation (Sokal and Rohlf 1981) used for variables 8-10, 14-16, 22-27; square root of basal area used on variables 11-13. Values for variables 22-38 based on 20 points placed 2 m apart along two 20-m orthogonal axes.

projection, the vegetation variables were standardized to a mean of 0 and standard deviation of 1 (Sneath and Sokal 1973).

Niche overlap and breadth.—We evaluated niche overlap and niche breadth relative to a habitat gradient extending from open areas to woodlands, which is represented (as detailed in the Results section) by principal component I. The habitat gradient represented by projections of the 194 nest boxes onto this component was subdivided into nine intervals, and we determined the number of nest boxes with projections from: (1) -0.74 to -0.5; (2) >-0.5 to -0.3; (3) >-0.3 to -0.1; (4) >-0.1 to 0.1; (5) >0.1 to 0.3; (6) >0.3 to 0.5; (7) >0.5 to 0.7; (8) >0.7 to 0.9; (9) >0.9 to 1.2. The numbers of nests for each species in each interval were tabulated.

Niche overlap was evaluated using the simplified Morisita index (M ; Krebs 1989) proposed by Horn (1966):

$$M = \left(2 \sum_{i=1}^n p_{ij} p_{ik} \right) / \left(\sum_{i=1}^n p_{ij}^2 + \sum_{i=1}^n p_{ik}^2 \right),$$

where p_{ij} is the proportion that resource i is of the total resources used by species j , p_{ik} is the proportion that resource i is of the total resources used by species k , and n is the total number of resource states. This index ranges from 0 when there is no overlap in resource use to 1 when there is complete overlap (when the two species use resources in equal proportions).

Niche breadth was assessed using Smith's index (B ; Krebs 1989):

$$B = \sum_{i=1}^n (p_i a_i)^{0.5},$$

where p_i is the proportion that resource i is of the total resources used by the species and a_i is the proportion that resource i is of the total resources available, and n is the total number of resource states. This index ranges from near 0 when only a single resource state is used (i.e., minimum breadth) to 1 when all resources are used in proportion to their availability (maximum breadth).

A Monte Carlo simulation was employed to evaluate the degree to which the resulting coefficients differed in a significant way statistically from what one would expect by chance alone. We started with the 194 nest boxes distributed among the nine resource states and randomly drew the number of nests for species j and then the number of nests for species k ; all were drawn without replacement. For the two groups of randomly drawn nests we then calculated the simplified Morisita index for niche overlap. This was compared with the value of the index for the two species as calculated from the actual samples of nests to determine whether the simulated value was less than the sample value, or greater than/equal to it. The simulation was repeated 1000 times and, based on the number of index values less than or greater than/equal to the sample value, we calculated the two-tailed probability that the sample value deviated from what would be expected by chance alone.

In a similar way we randomly drew from the 194 available nest boxes the number of nests for a given species without replacement and calculated the Smith index for niche breadth. As above, the simulation was repeated 1000 times, and we calculated the two-tailed probability that the sample value deviated from chance expectation.

Given that we are drawing without replacement the expected values for the simplified Morisita index and the Smith index increase as the numbers of nests in the samples increase. Thus, we are statistically evaluating whether a given value deviates significantly from the expected value for a given-sized sample.

Discriminant analysis.—Stepwise discriminant analysis (McLachlan 1992), also referred to by various authors as canonical-variate analysis, was used to determine the subset of the 40 vegetation variables that, in combination, maximally discriminated among sample plots for the different species, as well as for the unoccupied boxes. We used program 7M of the computer package BMDP (Dixon 1990) for calculations. As stated by Dixon (1990), the discriminant analysis in this program is one approach to one-way multivariate analysis of variance. Vegetation variables were selected that exhibited relatively high variation among species and low variation within species. Forward and backward stepping was used (i.e., variables were entered or removed from the classification function based on F -values). The F -to-enter a variable in the classification function was set at 4.0, while the F -to-remove was 3.996. Sample plots were projected onto the resulting canonical axes.

Classification functions were derived to assign plots to one of the groups, depending on

the relative probability of group membership. A given plot had an equal probability of being assigned to any one of the groups. Note this does not mean that an equal number of plots would be assigned to each group, but only that *a priori* we did not bias the possibility of a particular plot being categorized as representing one species or another. In fact, because sample sizes for species were unequal, more plots were assigned to some species than to others simply because plots had attributes that were characteristic of particular species. Measurement values for the plot were multiplied by coefficients of the classification function, and the resulting products added to the constants of these functions. The calculation was completed for all group members, and a plot assigned to the appropriate group, depending on which of the resulting classification values was the greatest (Schnell et al. 1986). We also used a true-jackknifed classification procedure, which effectively leaves out the individual plot being considered, recomputes coefficients of the functions, and then evaluates the plot. Typically, this procedure gives a better indication of the efficacy of functions to correctly allocate or identify new plots (i.e., those not used to compute the functions; Schnell et al. 1986).

As indicated by Morrison et al. (1992) and others, one must be judicious when interpreting discriminant analyses and other multivariate results where relatively small samples are involved for groups being evaluated. In our study the numbers of some species nesting in the area were relatively small. Thus, we have been cautious in our evaluation of discriminant analyses. Also, use of the jackknife procedure results in a conservative assessment of the degree of discrimination possible between species.

In order to assess the relationship, if any, between nest success and habitat measures, we plotted the percent fledged from eggs laid and percent fledged from eggs hatched against each of the three components. Least-squares regression analyses were used statistically to assess relationships.

RESULTS

Principal-components analysis.—The first 10 components had eigenvalues greater than one, while only the first four had eigenvalues greater than two. The first four principal components explained 56.2% of the total variance in vegetation variables, while the first three summarized 49.4%. Correlations of components with original variables and plot projections (Table 2, Figs. 1–3) indicate that component I (eigenvalue of 11.65; 29.1% of total variance) represents a gradient from open grassy areas (high negative loading for GRASSCOV) to oak forest areas (high positive loading for OAKB, BAOAK). In addition, the variables portraying vertical structure of the vegetation and percent ground cover of leaves (LEAFCOV, HITSE-HITSK, CANHT, VARCAN) exhibited high loadings on component I, reflecting the gradient from open to forested areas. Component II (eigenvalue of 4.29; 10.7% of total variance) represents a gradient of increasing numbers of deciduous species other than oaks (DENSJ, BANON, RDNON; Fig. 1). No other vegetation variables exhibited high loadings (Table 2). The loadings and projections on component III (Table 2, Fig. 1), which explained 9.6% of the total variance (eigenvalue of 3.85), reflect a gradient from wooded areas with junipers and few oaks (JUNA, DENSJ, BAJUN, RDJUN, STEMJ) to areas having

oaks and few junipers (BAOAK, DENSO, RDOAK). Component IV (6.7% of total variance) is a gradient from wooded areas with deciduous trees other than oaks and with few junipers (STEMN, HITSA, HITSC) to wooded areas with junipers but with few deciduous trees other than oaks (DENSJ, RDJUN). The eigenvalue for component IV was 2.68, which indicates that less than the equivalent of three original variables is summarized. Thus, we have not included projections or detailed loadings for this component.

When considering species individually, the plots for the nest boxes occupied by Bewick's Wrens have a broad range on component I (Fig. 2A); however, most of them have relatively high values on component I, indicating an association of Bewick's Wrens with more wooded areas. On component II, two-thirds of the plots have negative projections, which indicates a degree of avoidance of areas with relatively large numbers of deciduous trees other than oaks. On component III, Bewick's Wren plots are dispersed along the axis; however, two-thirds of the plots have negative values, indicating some degree of affinity for areas with junipers (Fig. 2B). Thus, Bewick's Wren plots, typically, were located in forested areas with junipers and relatively few deciduous tree species other than oaks.

Carolina Chickadee nest boxes tended to be in more open areas containing relatively few trees, as indicated by projections on component I (Fig. 2C), although the affinity for open areas was not as pronounced as in the Eastern Bluebird (Fig. 3A) and House Sparrow (Fig. 3C). Chickadee plots are widely distributed on component II (Fig. 2D), suggesting that this species shows no preference with respect to deciduous species other than oaks. However, chickadee plots have intermediate values on component III, indicating a preference for areas with mixed junipers and oaks (Fig. 2D). In general, Carolina Chickadee plots were found in open areas interspersed with juniper and oak trees. The broad distribution of Tufted Titmouse plots on component I (Fig. 2E) indicates no preference for open or forest habitats. However, 72% of the nest boxes used by Tufted Titmice have positive values on component III (Fig. 2F), indicating they were found in areas with oaks and relatively few junipers.

Plots occupied by Eastern Bluebirds are concentrated in grassy areas with few trees, as indicated by projections on component I (Fig. 3A). Not unexpectedly, given their known preference for open areas, no strong associations with deciduous trees or junipers are demonstrated (Fig. 3A, B). Nest boxes selected by House Sparrows were located in open grassy habitat as indicated by projections on component I (Fig. 3C). However, no other strong patterns were discernable with respect to variables summarized by components II and III (Fig. 3C, D). The unoccupied plots

TABLE 2
 PRINCIPAL-COMPONENT LOADINGS AND RESULTS OF PRINCIPAL-COMPONENTS ANALYSIS BASED ON 40 VEGETATIONAL VARIABLES^a

Variable	Component			Variable	Component		
	I	II	III		I	II	III
1 OAKA	0.394	-0.280	0.379	21 STEMV	0.268	0.167	-0.197
2 OAKB	0.605	0.070	0.420	22 WOODYCOV	0.420	-0.032	0.068
3 OAKC	0.165	-0.087	0.176	23 FORBCOV	0.463	0.340	-0.083
4 NONA	0.560	0.412	-0.201	24 GRASSCOV	-0.818	-0.229	-0.130
5 NONB	0.407	0.437	-0.009	25 LEAFCOV	0.669	0.060	0.196
6 NONC	-0.071	0.286	-0.114	26 ROCKCOV	0.003	0.149	0.015
7 JUNA	0.501	-0.315	-0.415	27 BARECOV	0.203	0.176	0.337
8 DENSO	0.373	-0.335	0.671	28 HITSA	0.398	0.011	-0.102
9 DENSN	-0.020	0.741	-0.305	29 HITSB	0.527	-0.200	-0.187
10 DENSJ	-0.053	-0.492	-0.420	30 HITSC	0.573	-0.345	-0.367
11 BAOAK	0.762	-0.128	0.481	31 HITS D	0.588	-0.354	-0.366
12 BANON	0.547	0.635	-0.189	32 HITSE	0.641	-0.312	-0.385
13 BAJUN	0.498	-0.389	-0.517	33 HITSF	0.725	-0.201	-0.279
14 RDOAK	0.516	-0.369	0.648	34 HITS G	0.700	-0.146	-0.170
15 RDNON	-0.131	0.747	-0.362	35 HITS H	0.809	-0.026	-0.149
16 RDJUN	-0.148	-0.459	-0.440	36 HITS I	0.783	0.128	0.060
17 VARQUAD	0.583	-0.103	-0.127	37 HITS J	0.750	0.281	0.131
18 STEMO	0.387	-0.413	0.314	38 HITS K	0.709	0.302	0.173
19 STEMN	0.399	0.217	-0.273	39 CANHT	0.839	0.275	0.162
20 STEMJ	0.491	-0.234	-0.439	40 VARCAN	0.840	0.174	0.042

^a Relatively high loadings highlighted in bold as follows: (component I) > |0.6|; (component II) > |0.5|; (component III) > |0.4|.

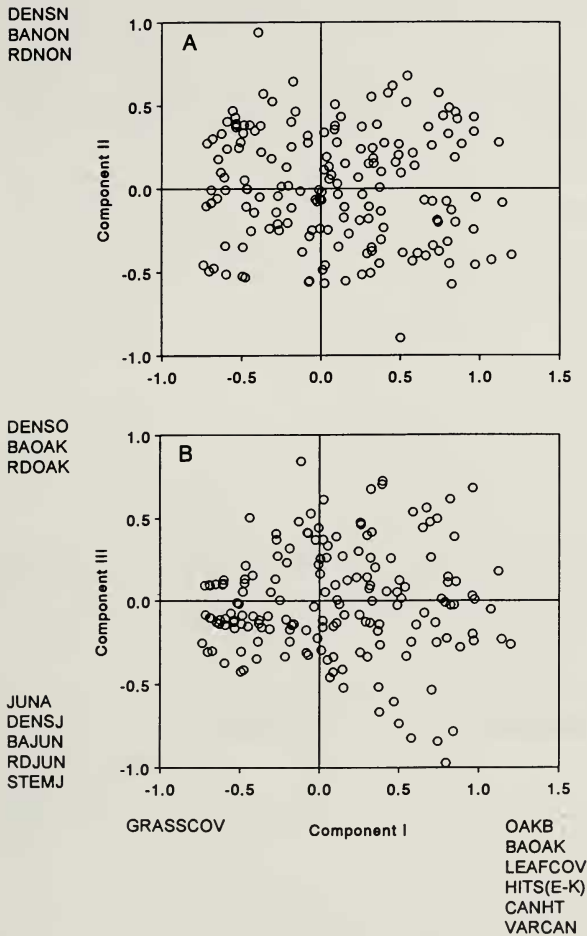


FIG. 1. Projections of all 194 sample plots (for five species and for unoccupied sites) onto principal components based on 40 vegetation variables: (A) components I and II; (B) components I and III. Codes indicated for variables with high positive or negative loadings on particular axes.

were broadly distributed on all three principal-component axes (Fig. 3E, F). Since the study areas were “saturated” with nest boxes, it is not unexpected that projections of unoccupied plots were distributed through a variety of habitats.

Measures of reproductive success were calculated (i.e., percent fledged from eggs laid and percent fledged from eggs hatched) and analyzed with respect to projections onto components I, II, and III for all occupied nest

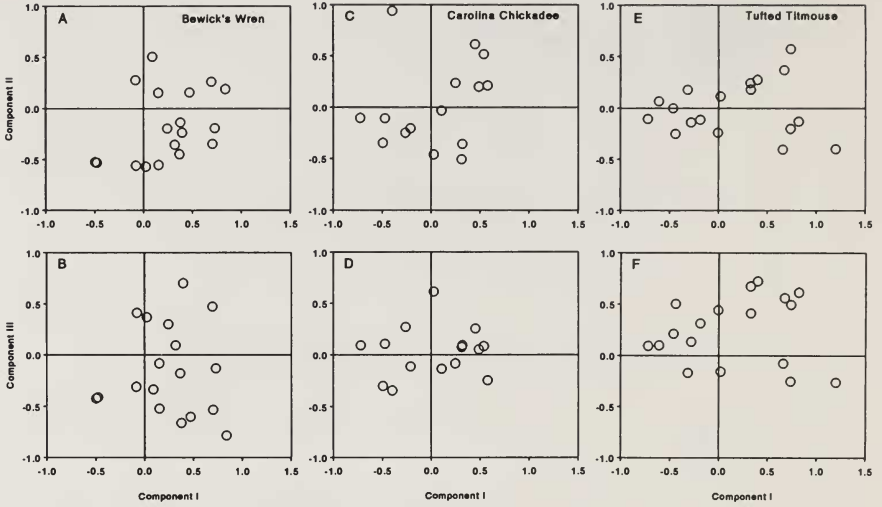


FIG. 2. Projections for (A–B) Bewick's Wrens, (C–D) Carolina Chickadees, and (E–F) Tufted Titmice onto principal components I, II, and III resulting from analysis of all 194 sample plots and 40 vegetation variables.

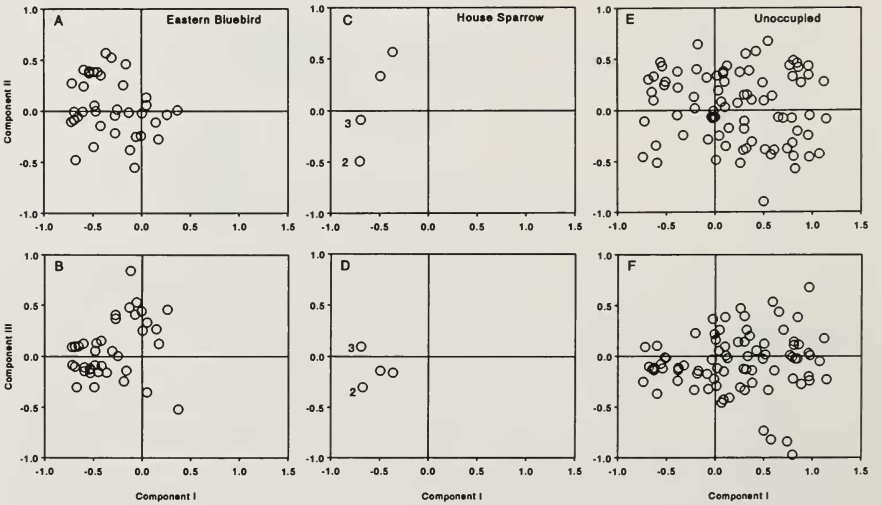


FIG. 3. Projections for (A–B) Eastern Bluebirds, (C–D) House Sparrows, and (E–F) unoccupied plots onto principal components I, II, and III resulting from analysis of all 194 sample plots and 40 vegetation variables. Numbers in panels C and D denote placement of an indicated number of overlapping points.

boxes. Reproductive success exhibited no correlation with component projections for any of the five species.

Niche overlap and breadth.—Our analyses of niche overlap and breadth involve the distributions of nests of particular species along principal-component I (Fig. 4), which is a composite vegetation measure with low values indicating open habitats and high values indicating relatively dense woodland. The 194 nest boxes were placed in nine categories based on their projections onto principal component I. As indicated by the forward-most graph in Fig. 4, the boxes were distributed relatively uniformly along the first principal component, with a slightly greater proportion occurring at the open end of the spectrum and slightly fewer at the woodland end.

The 18 Bewick's Wren nests were distributed over much of the component's range, although the wrens did not use boxes in the most open habitat or in the dense woodland (Fig. 4; see also Fig. 2A). The 15 Carolina Chickadee nests also were found along much of the gradient, although the species did not use boxes in the two categories representing the densest woodland available (Fig. 2C). The 19 nests of the Tufted Titmice were nearly uniformly distributed along the habitat gradient, while the 50 Eastern Bluebird nests were found in more open areas, with almost half occurring in nest boxes in the category representing the open extreme of the habitat gradient (Fig. 3A). All of the nine House Sparrow nests were in boxes in the two categories including nest boxes placed in the most open areas (Fig. 3C).

Niche-overlap values using the simplified Morisita index ranged from 0.058 for the Bewick's Wren and House Sparrow to 0.866 for the Eastern Bluebird and House Sparrow (top of Table 3; species ordered on the basis of number of nests found). As indicated in the Methods, when sampling without replacement, the expected overlap values are higher for species where one or both had a relatively large number of nests. Thus, the expected values (see simulation means in middle of Table 3) range from 0.645 for the Carolina Chickadee and House Sparrow to 0.812 for the Eastern Bluebird and Tufted Titmouse.

Statistically significant negative deviations (bottom section of Table 3), which indicate less overlap than predicted on the basis of chance alone, were found for House Sparrow (graph 5 in Fig. 4) with the Carolina Chickadee, Bewick's Wren, and Tufted Titmouse (graphs 1–3 in Fig. 4). This is particularly marked for the comparison with the Bewick's Wren, a species not found nesting in the most open areas (see far left of graph 1 in Fig. 4). A similar pattern of significant negative deviations was found for the Eastern Bluebird (graph 4 in Fig. 4) with the Carolina Chickadee, Bewick's Wren, and Tufted Titmouse (bottom line in Table 3). Not sur-

TABLE 3
 NICHE OVERLAP BETWEEN SPECIES PAIRS AS INDICATED BY SIMPLIFIED MORISITA INDEX.
 ACTUAL VALUE, MEAN VALUE FOR 1000 SIMULATIONS USING SAME SAMPLE SIZES, AND
 DEVIATION OF SIMULATED FROM ACTUAL^{a,b}

Species	House Sparrow	Carolina Chickadee	Bewick's Wren	Tufted Titmouse
Actual overlap (M)				
Carolina Chickadee	0.230			
Bewick's Wren	0.058	0.800		
Tufted Titmouse	0.400	0.706	0.702	
Eastern Bluebird	0.866	0.425	0.250	0.617
Simulated overlap (\bar{M}_s)				
Carolina Chickadee	0.645			
Bewick's Wren	0.656	0.720		
Tufted Titmouse	0.655	0.731	0.743	
Eastern Bluebird	0.706	0.782	0.809	0.812
Deviation ($M - \bar{M}_s$)				
Carolina Chickadee	-0.414**			
Bewick's Wren	-0.598***	0.080 ns		
Tufted Titmouse	-0.255*	-0.025 ns	-0.041 ns	
Eastern Bluebird	0.160*	-0.357**	-0.559***	-0.195*

^a Species arranged by sample size: House Sparrow (9), Carolina Chickadee (15), Bewick's Wren (18), Tufted Titmouse (19), and Eastern Bluebird (50).

^b ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

prisingly, there is a significant positive deviation in the overlap value for the Eastern Bluebird and House Sparrow (Table 3; graphs 4 and 5 of Fig. 4), indicating that they are more likely to be found together in the same habitat (i.e., open areas) than expected by chance. The habitat-overlap values involving all pairs of three species (i.e., Carolina Chickadee, Bewick's Wren, and Tufted Titmouse) do not deviate significantly from values expected simply by chance (bottom section of Table 3).

For niche breadth, the calculated Smith index (B) ranged from 0.596 for the House Sparrow to 0.937 for the Tufted Titmouse (Table 4). The species in Table 4 have been ordered on the basis of the number of nests and, as indicated by the mean simulated values (\bar{B}_s), the niche breadth value increases as the sample increases, since sampling is done without replacement. For three species, the negative deviations from expected values were statistically significant (Table 4). The House Sparrow and Eastern Bluebird were restricted to the open habitats, while Bewick's Wrens more often nested in semiopen areas (Fig. 4) than predicted by chance. For the Carolina Chickadee and Tufted Titmouse, nest-box use

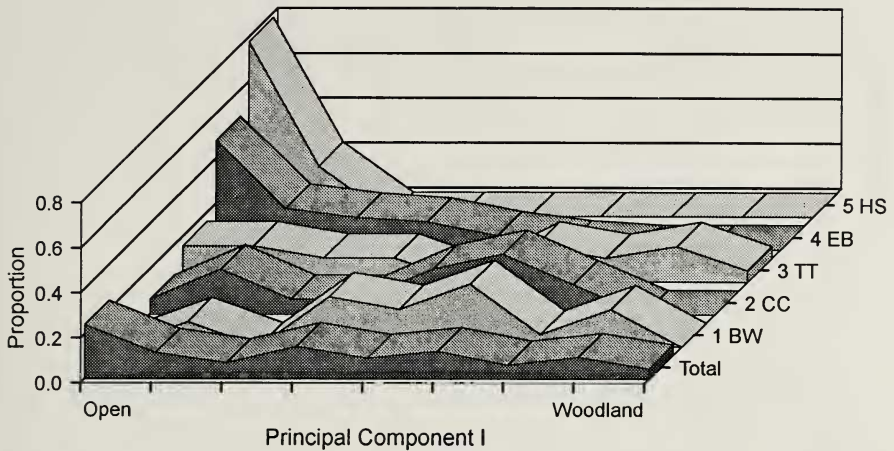


FIG. 4. Groupings of projections onto principal component I for each species into nine categories, with proportions in each group for each species indicated. Proportions of all nest boxes (194 total) in each category denoted in foremost graph.

relative to this habitat gradient was not different from random expectations.

Discriminant analysis.—Canonical variables provided separation of nest sites occupied by the different species (Fig. 5). Each plot was assigned to one species using classification functions developed in the stepwise discriminant analysis (top of Table 5). The greatest accuracy with respect to correctly classifying a given nest as having been used by a particular species was achieved for plots occupied by Eastern Bluebirds, with 70.0% correctly classified (Table 6). Approximately one-half of the plots occupied by Bewick's Wrens and Carolina Chickadees were clas-

TABLE 4
NICHE BREADTH AS INDICATED BY SMITH INDEX^a

Species	No. nests	B	B_s	$B - B_s$
House Sparrow	9	0.596	0.806	-0.210**
Carolina Chickadee	15	0.857	0.890	-0.033 ns
Bewick's Wren	18	0.790	0.910	-0.120**
Tufted Titmouse	19	0.937	0.919	0.018 ns
Eastern Bluebird	50	0.844	0.982	-0.138***

^a Actual value (B), mean value (B_s) for 1000 simulations using same sample size, and deviation of simulated from actual ($B - B_s$).

^b ns, $P > 0.05$, **, $P < 0.01$, ***, $P < 0.001$.

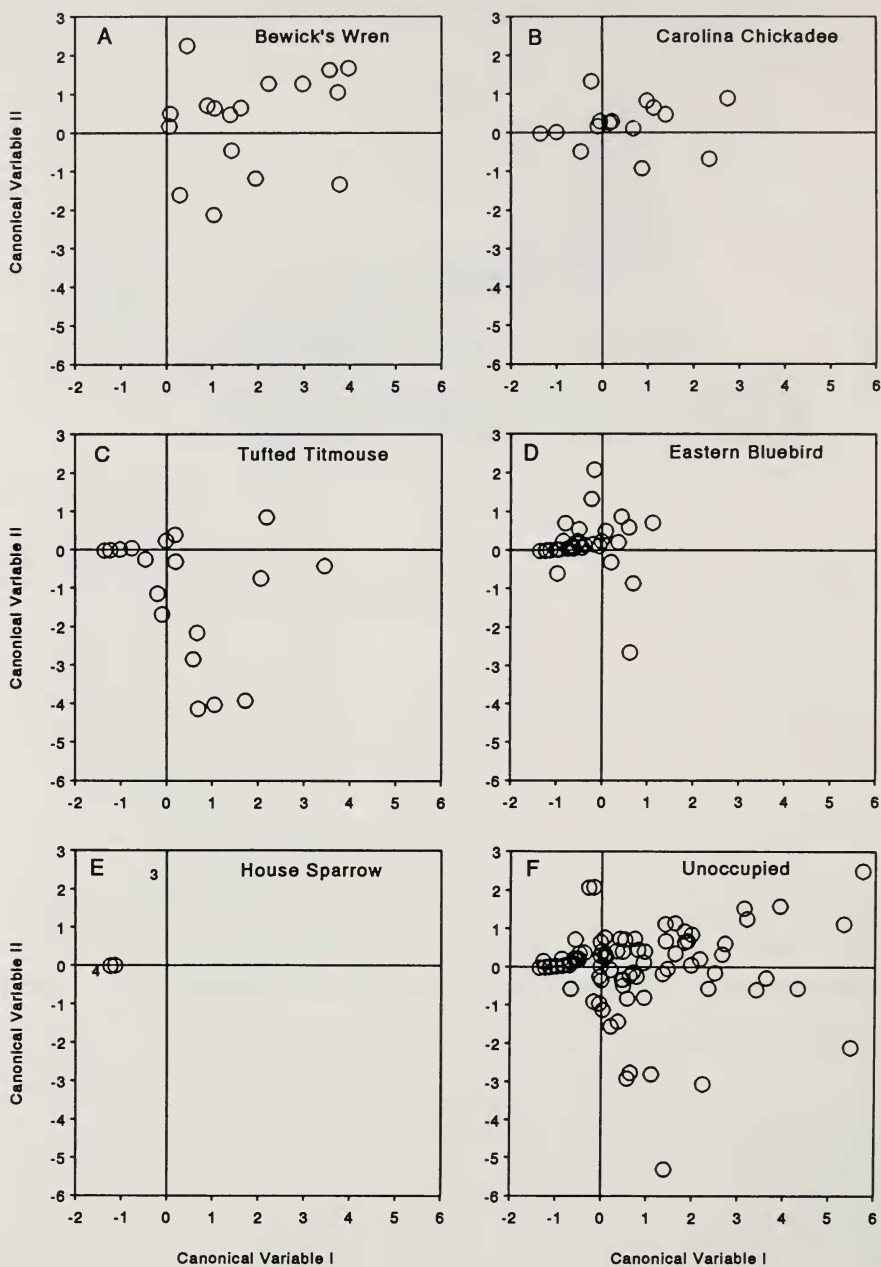


FIG. 5. Projections of sample plots for each species and unoccupied plots on canonical variables I and II: (A) Bewick's Wren; (B) Carolina Chickadee; (C) Tufted Titmouse; (D) Eastern Bluebird; (E) House Sparrow; (F) unoccupied plots. Numbers in panel E denote placement of an indicated number of overlapping points.

TABLE 5
STATISTICS FOR STEPWISE DISCRIMINANT ANALYSES OF PLOTS

Variable	F-value to enter	Order of entry	Standardized canonical-variable coefficients				Classification function ^a				
			1	2	3	4	BW	CC	TT	EB	HS
HITSD	15.92	1	0.343	-0.818	-0.458	-0.167	0.996	0.209	0.252	0.013	-0.050
OAKB	8.39	2	0.218	0.475	-0.618	-0.592	0.552	0.157	1.132	0.054	0.044
VARQUAD	4.79	3	0.704	0.191	-0.267	0.701	0.858	1.112	0.258	0.438	0.157
DENSJ	4.08	4	0.413	0.040	0.760	-0.592	3.246	1.611	0.873	0.778	4.048
Constant			-1.347	-0.026	-0.193	0.641	-6.518	-4.184	-3.824	-1.978	-2.708
All species except House Sparrow											
HITSD	17.95	1	0.748	0.184	0.709	—	0.923	0.193	0.233	0.012	—
OAKB	9.67	2	0.347	-0.949	0.009	—	0.456	0.118	1.031	0.037	—
VARQUAD	4.78	3	0.388	0.282	-0.936	—	0.806	1.039	0.546	0.409	—
Constant			-1.279	0.005	0.668	—	-5.302	-3.623	-3.391	-1.693	—

^aSpecies codes: BW, Bewick's Wren; CC, Carolina Chickadee; TT, Tufted Titmouse; EB, Eastern Bluebird; HS, House Sparrow. Tabulated values used with original values for variable Products of corresponding measurements and function values summed and then added to constant. Plot classified into particular group based on which classification function produces it highest value.

TABLE 6
CLASSIFICATION OF PLOTS USING STEPWISE DISCRIMINANT ANALYSIS^a

Group	Percent correctly classified	Classified as				
		BW	CC	TT	EB	HS
All plots						
Bewick's Wren (BW)	55.6	10	4	2	0	2
Carolina Chickadee (CC)	53.3	3	8	0	3	1
Tufted Titmouse (TT)	36.8	3	2	7	7	0
Eastern Bluebird (EB)	70.0	3	7	2	35	3
House Sparrow (HS)	33.3	0	0	0	6	3
Unoccupied plots	—	23	19	13	25	3
All species except House Sparrow						
Bewick's Wren	50.0	9	5	2	2	—
Carolina Chickadee	60.0	2	9	0	4	—
Tufted Titmouse	36.8	3	3	7	6	—
Eastern Bluebird	74.0	2	9	2	37	—
House Sparrow ^b	—	0	0	0	9	—
Unoccupied plots	—	26	18	12	27	—

^a Standard classification and jackknife classification were the same.

^b For this analysis, House Sparrow plots not used in canonical-variate analysis, but then classified *a posteriori* into one of the other species.

sified correctly (55.6 and 53.3%, respectively). However, only one-third of Tufted Titmouse and House Sparrow plots were correctly assigned (36.8 and 33.3%, respectively). The unoccupied plots also were classified by the functions derived from stepwise discriminant analysis. All species were evenly represented by the classification of unoccupied plots with the exception of the House Sparrow. Only three of the unoccupied plots were classified as being typical for House Sparrows (Table 6).

Stepwise discriminant analysis was repeated, with plots occupied by House Sparrows entered as unknowns to determine if classification accuracy for plots was affected by the inclusion of House Sparrow plots. The resulting classification function is given in Table 5 (bottom). This analysis provides information on the potential effects of an introduced species on nest-site selection of native species. All plots including those occupied by House Sparrows were classified into the remaining four species groups. As in the previous analysis, the greatest classification accuracy was attained for plots occupied by Eastern Bluebirds, with 74.0% correctly classified (bottom of Table 6), 4% higher than when House Sparrow plots were included in a separate group. Classification accuracy also increased for plots used by Carolina Chickadees, with 60.0% correctly classified. The percentage of Tufted Titmouse plots correctly clas-

sified remained the same (36.8%). Correct classification of plots occupied by Bewick's Wrens decreased 5.6% to 50.0%. All of the plots used by House Sparrows were assigned as Eastern Bluebird plots (bottom of Table 6). The unoccupied plots were assigned to species groups, with 32.5% of plots identified as Eastern Bluebird plots and 14.5% identified as Tufted Titmouse plots. The modest increases in classification accuracy reflect the overlap of habitat preferences.

In both discriminant analyses, the number of decimeters with tree hits in the >1.5–2.0-m height zone (HITSD), the number of oaks with dbh >22.5–52.5 cm (OAKB), and the standard deviation of the number of trees per quadrant (VARQUAD) were the first three variables entered (Table 5). The first analysis, which involved all groups, also included the density of junipers (DENSJ) as the fourth variable. Thus, the vegetation at lower heights (HITSD, DENSJ) and vegetation density (VARQUAD, DENSJ) are, in combination, the most useful nesting-habitat characteristics to distinguish among these five secondary cavity-nesting species.

DISCUSSION

Species preferences.—The general vegetational gradients calculated in our study were quite similar to those obtained by James (1971) in an evaluation of Arkansas breeding birds. Component I in both studies represented a gradient from open grassy areas to wooded areas. Our component III reflects a strong gradient from decreasing junipers to increasing oaks. Although junipers were not separated from other trees in variables used in the Arkansas study, the compact shape of junipers is reflected structurally by the dense shrubs represented on component II of the James study, which was a gradient from dense shrubs to medium-sized trees and few shrubs.

Results from stepwise discriminant analysis in the Arkansas study indicated that the discriminant axes represented a continuum from open country to forest associations, and one from upland to bottomland areas (James 1971). Carolina Chickadees and Tufted Titmice exhibited high values on the discriminant axis, indicating their strong association with wooded areas. These results differ somewhat from our findings in that Carolina Chickadee plots in our study areas primarily were located in areas with scattered trees. In our study, Tufted Titmice nests were not restricted to heavily wooded areas, but also were found in open areas with few trees. Bent (1946) described the general breeding habitat of chickadees and titmice as being the forest edge, but noted that Tufted Titmice occasionally nest along borders of fields and in open pastures. The niche-breadth index we calculated also indicates that titmice exhibit a broad range of habitat use.

Posey (1974), characterizing the habitats of breeding birds in Ozark shrubby old fields, demonstrated vegetational patterns similar to those found in our study. He evaluated 16 vegetational characters to describe the structural features of avian breeding habitats, using as focal points the song-perch sites. From principal-components analysis, he found that component I represented a vegetational biomass gradient (i.e., a gradient from open grassy fields to shrubby wooded areas). Component III showed strong correlations with shrub density and canopy variables, indicating a gradient from dense shrubs to wooded areas with little understory. Among the species evaluated, Posey (1974) found that Eastern Bluebird plots had low values on component I, indicating the strong preference of this species for open grassy areas. Eastern Bluebird nest sites described in our study also suggest that the species has a strong preference for open grassy areas. Our simulation results indicate Eastern Bluebirds have a relatively narrow niche breadth. For this species, habitat characteristics of song-perch sites (Posey 1974) and nest-box sites (our study) were very similar. Several studies (e.g., Bent 1949; Zeleny 1976; Pinkowski 1976, 1977, 1978) also have shown that breeding Eastern Bluebirds prefer forest edges and open areas with scattered trees. Willner et al. (1983) noted that bluebirds selected nest sites in areas of poor soils where herbaceous vegetation was sparse or where mowing had recently occurred.

Whitmore's (1975) habitat-ordination study of passerine birds of the Virgin River Valley in southwestern Utah incorporated discriminant-function analyses to determine the most important characters that, in combination, would distinguish among species. As with most other avian habitat-ordination studies, he found that the first discriminant axis represented a gradient from low canopy cover to densely forested areas. Among the species evaluated, Bewick's Wrens were located midway along the discriminant axis; they showed a preference for relatively open areas interspersed with trees. In our study, Bewick's Wren plots were more closely associated with wooded areas containing junipers. Bent (1948) indicated that, although the Bewick's Wren is found in a variety of habitats (including open woodlands, upland thickets and fence rows), the nests often are well concealed (e.g., in the center of dense brush). A possible explanation for the differences in habitat characteristics shown for perch sites (Whitmore 1975) and nest sites (our study) is that the female selects areas with more vegetation near the nest site to provide protection and to make the nest relatively inconspicuous. However, the song-perch sites, located by singing males, are in more open areas, which provide increased visibility for (and of) displaying males.

Conner et al. (1983) used principal-components and discriminant analyses to ordinate breeding habitat of bird species on vegetational continua

in eastern Texas. They found Tufted Titmice most often in wooded areas and those with relatively large numbers of shrubs. Carolina Chickadees were also closely associated with wooded areas, but preferred open understories. In our study, Carolina Chickadees preferred areas that were relatively open with scattered trees, and Tufted Titmouse plots were broadly distributed showing no particular association with open or wooded areas.

Interspecific competition.—Native species are not only influenced by human disturbances, but by introduced species such as the House Sparrow and European Starling (*Sturnus vulgaris*). Since their introduction, these species have invaded much of North America (Zeleny 1976). Cavity nesters are particularly vulnerable to the aggressive nature of these species, which may compete for available nest sites. European Starlings did not affect birds using our nest boxes, because the entrance hole was too small for starlings to enter. However, House Sparrows were not prevented from usurping nest boxes. The native species most affected by House Sparrows in our study appears to be the Eastern Bluebird. As illustrated in one of the stepwise discriminant analyses (bottom of Table 6), all plots occupied by House Sparrows were classified as Eastern Bluebird plots, indicating the similarities between nest sites of these two species. In addition, simulation results showed substantial overlap for House Sparrows and Eastern Bluebirds. Willner et al. (1983) investigated nest-box use and habitat characteristics in Maryland employing an alternate set of environmental variables. Using discriminant functions, they found that five of six nest boxes occupied by House Sparrows were in habitats favored by bluebirds.

In our study, seven of nine nest boxes used by House Sparrows were initially occupied by Eastern Bluebirds. In addition, we have direct evidence of competition occurring between the two species with Eastern Bluebirds being detrimentally affected. On 14 May and 25 May 1990, a House Sparrow was observed displacing a male Eastern Bluebird. In both cases a male bluebird was found dead in the nest box on the following day (Pogue, pers. obs.). Carter (1981), conducting studies in the same area of Oklahoma, also found that House Sparrows displaced bluebirds during nesting, and Zeleny (1976) noted that House Sparrows are exceptionally aggressive and usually can displace bluebirds from a particular site. Although the Eastern Bluebird population has increased over most of its range in recent years (Sauer and Droege 1990), continued growth of the House Sparrow population in rural areas could negatively affect Eastern Bluebird populations due to the similarity of nest sites selected by the two species and the aggressive nature of House Sparrows.

Characteristics of simulation approach used.—The niche-breadth and overlap simulations were helpful in comparing and contrasting species. These analyses support the suggestion that nest-box use by House Sparrows and Eastern Bluebirds is significantly more similar than expected by chance. This point was demonstrable in spite of the relatively limited number of House Sparrow pairs using nest boxes in the study areas. Not surprisingly the simulations also showed House Sparrows and Eastern Bluebirds to be markedly different from the other three species in their choice of nest boxes along the general gradient summarizing the degree of habitat openness.

Simulations by their very nature have limitations. When initiating such an analysis, it is necessary to make decisions concerning the extent to which a simulation model should directly reflect nature. Often there is a trade-off involving generality versus closeness of fit to a particular situation. We based habitat categories on the projections of nest boxes onto principal component I and, thus, confined the analysis to those habitat characteristics summarized by this component. A more elaborate simulation involving groups based on more components likely would have shown the Bewick's Wren to have less habitat overlap with the Tufted Titmouse and Carolina Chickadee, since the overall principal-component analysis indicated that the wren has an affinity for areas with junipers (relevant characteristics summarized on principal component III). At the same time, detailing more habitat aspects in the simulation could have obscured the extent to which overlap is evident when one focuses on the degree of habitat openness. We made the conscious decision to analyze only component I because it represented an important and general habitat descriptor—a readily understandable dimension worthy of special attention because it summarizes a basic continuum separating habitats of the region.

Two other aspects of our simulation model deserve comment. First, we deliberately sampled without replacement when establishing an expected distribution across habitats for a given species. Even though not all nest boxes were occupied, only a certain number were available (just as only a finite number of natural cavities exist in a particular area). Since nest boxes represented a limited resource, this seemed to be the most appropriate approach. In terms of the number of nest boxes potentially available to a particular species or a particular pair, our model was not totally realistic since the birds and nest boxes in the field were evaluated over two seasons, while we set up the simulation as if a single season were involved; given the clear-cut simulation results we do not believe that this simplification detracts from the general findings.

Second, our simulations (and the measures of niche overlap and

breadth) were based on discrete, unordered habitat categories, while in fact the nine groupings can be ordered (i.e., they represent portions of a subdivided continuum). The main effect of using unordered categories probably was to make statistical tests somewhat more conservative than would have been the case if ordered categories had been employed (along with appropriate coefficients); with ordering, a coefficient would take into account the fact that species tended to have similar frequencies in adjacent habitat categories. Additional simulations with more elaborate assumptions could be helpful in further elucidating habitat relationships of these birds. The simulations reported here were useful in clarifying interspecific associations and helping us to understand the expected values for niche breadth and overlap given a limited resource (i.e., nest boxes).

Concluding remarks.—The quantitative findings obtained through our analyses reflect the general qualitative descriptions in the literature of breeding habitats for these secondary cavity-nesting species. For example, breeding sites of Bewick's Wrens are generally described as being located in brushy areas along the forest edge (Bent 1948). Carolina Chickadees and Tufted Titmice are associated with deciduous and mixed deciduous-juniper woodlands (Ehrlich et al. 1988); however, as pointed out earlier, Bent (1946) noted that the Tufted Titmouse sometimes nests along borders of fields and in open pastures. Zeleny (1976) indicated that Eastern Bluebirds prefer breeding sites in open country with scattered trees and forest edge. House Sparrow breeding sites are most often located near human habitation; however, in rural areas, House Sparrows select nest sites in any available cavity, including nest boxes (Summers-Smith 1963).

Overall, for our analyses, nest sites of the species studied can be characterized on a gradient, with Bewick's Wrens preferring nest sites in wooded areas containing junipers, and Carolina Chickadees selecting areas mixed with junipers and oak trees. Tufted Titmice selected nest sites in both open and wooded areas; however, plots found in wooded areas that were used by Tufted Titmice contained few junipers and deciduous trees other than oaks. Eastern Bluebirds and House Sparrows preferred sites in open grassy areas with few trees.

Clearly, our investigation and those of others indicate marked differences in habitat preferences of cavity-nesting species. For a nongame manager wanting to accommodate particular cavity-nesting species, nest boxes should be placed within the appropriate interval along the main habitat gradient. Zeleny (1976) noted that nest boxes in habitat suitable for Eastern Bluebirds but placed relatively near buildings would, not surprisingly, have a greater probability of attracting House Sparrows. For Eastern Bluebirds and House Sparrows, our data indicate that there are virtually no differences in the habitat characteristics of nest boxes select-

ed, a conclusion also reached by Willner et al. (1983). It is evident that these two species prefer very similar sites.

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